THE COMPARATIVE POLLINATION AND FLORAL BIOLOGY OF BAOBABS (*ADANSONIA*–BOMBACACEAE)[1]

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ABSTRACT

The baobabs comprise eight species with large, spectacular, nocturnal flowers. The African baobab, *Adansonia digitata*, has long been known to be bat-pollinated. In this paper I document the floral biology and pollination systems of the remaining seven species. The two species in section *Brevitubae*, both endemic to Madagascar, are pollinated by nocturnal mammals (fruit bats and lemurs). In contrast, the five species in section *Longitubae*, four endemic to Madagascar and one to Australia, are pollinated by long-tongued hawkmoths. In all cases, animals besides the legitimate pollinators also exploited nectar and pollen. The two pollination systems occurring in the genus correlate closely with differences in the floral morphology, phenology, and nectar production.

The baobabs comprise eight species in the genus *Adansonia* L. (Bombacaceae), six endemic to Madagascar, one to northwestern Australia, and one originally from continental Africa that has been dispersed by humans elsewhere in the tropics (Wickens, 1983). They are tropical trees growing in savanna, deciduous forest, or, rarely, moist, semi-evergreen forest. The genus is characterized by massive, often bottle-shaped trunks, palmately compound leaves, and a large, dry, indehiscent fruit containing reniform seeds embedded in an edible pulp. All species of *Adansonia* have large, spectacular flowers, but there are great differences in their floral biology. This variation is partially reflected in the subgeneric classification, with the three sections differing in the shape of the floral bud, orientation of the flower, and length of the staminal tube (Hochreutiner, 1908; Baum, 1995). The African baobab (*A. digitata* L.) is the sole representative of section *Adansonia*. Two Malagasy species (*A. grandidieri* Baill. and *A. suarezensis* H. Perr.) constitute section *Brevitubae*. The Australian species (*A. gibbosa* (A. Cunn.) Baum ex Guymer) and four Malagasy species (*A. rubrostipa* Jumm. & H. Perr., *A. madagascariensis* Baill., *A. za* Baill., and *A. perrieri* Capuron) constitute section *Longitubae*.

In the early part of this century, African baobabs growing in botanical gardens in the Far East were used to support the then heterodox assertion that tropical bats were important pollinators of some tropical plants. Van der Pijl (1934) inferred from the descriptions of van Harreveld-Lako (1926) that *A. digitata* was bat-pollinated; this prediction was

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confirmed in Java by Porsch (1935) and van der Pijl (1936). Ten years later Jaeger (1945, 1950, 1954) completed the first study of bat-pollination in natural populations of *A. digitata* in West Africa. He observed and carefully described the floral morphology and course of anthesis and recorded the visits of fruit bats (*Eidolon helvum* Kerr) to the flowers. Jaeger's thorough work demonstrating bat-pollination in *A. digitata* has been confirmed by many subsequent studies (e.g., Harris & Baker, 1959; Start, 1972; Ayensu, 1974), with three species of fruit bat (*Eidolon helvum*, *Epomorphorus gambianus* Ogilby, and *Rousettus aegyptiacus* E. Geoffroy) identified as major pollinators.

Agents other than fruit bats have been suggested to play a role in the pollination of *A. digitata*. Jaeger (1945) proposed wind-pollination, but this is unlikely because the pollen is not particularly light and the stigmatic area is small. In addition, bushbabies (*Otolemur crassicaudatus* E. Geoffroy and *Galago senegalensis* E. Geoffroy) visit *A. digitata* and could contribute somewhat to pollination (Coe & Isaac, 1965; Wickens, 1983). However, they are infrequent visitors and are destructive to flowers (Wickens, 1983), so their net effect on reproductive output is likely to be negative. Although it is possible that ants steal nectar, Humphries (1982) is mistaken in suggesting that *A. digitata* is ant-pollinated.

In contrast to the extensive information on the pollination of *A. digitata*, the Malagasy and Australian species are very poorly known. Little fieldwork has been undertaken prior to this study and no nocturnal observations have been reported. Nonetheless, several workers have made predictions about the pollination of the other baobabs. Van der Pijl (1956) and J. Armstrong (1979) assumed that, like *A. digitata*, the other baobabs would prove to be bat-pollinated. However, the striking differences in the floral morphology of *A. digitata* from the rest of the genus make this inference questionable. Werth (1915) suggested that *A. madagascariensis* was bird-pollinated. Similarly, Patrick Armstrong (1983) argued against bat-pollination in *A. gibbosa* and, having observed visits by birds (P. Armstrong, 1977), suggested that it and all the Malagasy baobabs might be bird-pollinated. This view seemed to gain support from reports of red and yellow flowers in the Malagasy species, these colors being typical of ornithophilous flowers (Faegri & van der Pijl, 1979). However, he made no nocturnal observation of *A. gibbosa* and was unable to study any of the Malagasy species in the field (P. Armstrong, pers. comm.). Here I report on the results of extensive field studies aimed at documenting the pollination and floral biology of the baobabs of Madagascar and Australia.

Methods and Materials

The fieldwork was carried out during the course of four trips to Madagascar and one to Australia between October 1987 and December 1991. A brief trip to Kenya in January 1989 allowed observation of bat visits to *A. digitata*. The dates and locations of the work are given in Table 1. Figure 1 shows the distribution of the main study sites in Madagascar. At each site I studied the floral biology of 2–25 trees and made pollination observations on 2–5. I was careful to select trees near the center rather than at the periphery of the population and ones that had abundant, accessible flowers. Throughout my work access to the canopy was achieved using the method described by Perry (1978).

FLORAL BIOLOGY

Most floral traits were scored on the basis of simple observation and measurement of fresh flowers. Here I will present only those characters that potentially influence pollination; general floral characteristics are described elsewhere (Baum, 1995).

Phenological data were derived from field observations and herbarium labels. In the case of *A. rubrostipa*, a more detailed study of 25 trees visible from a trail in Kirindy Forest was conducted. These trees were revisited daily for 15 days (February 10–25) and the number of freshly opened flowers recorded.

Nectar was extracted from flowers and its volume measured using microcapillary tubes. In sections *Adansonia* and *Brevitubae* the nectar was easily accessible. In section *Longitubae* the capillary tubes were carefully inserted between the petal bases. Unless otherwise stated, flowers were bagged from anthesis until the last nectar sample was taken.

The time course of nectar production was determined for *A. rubrostipa*, *A. grandidieri*, *A. za*, *A. perrieri*, and *A. gibbosa*. Initially, this was completed by making repeated measurements from the same flowers. This worked successfully with *A. grandidieri*, but when used on *A. rubrostipa* it seemed to damage the nectariferous tissue. To avoid these problems, in the three other species (*A. gibbosa*, *A. za*, and *A. perrieri*) samples of flowers were collected at each time interval and nectar was extracted destructively.

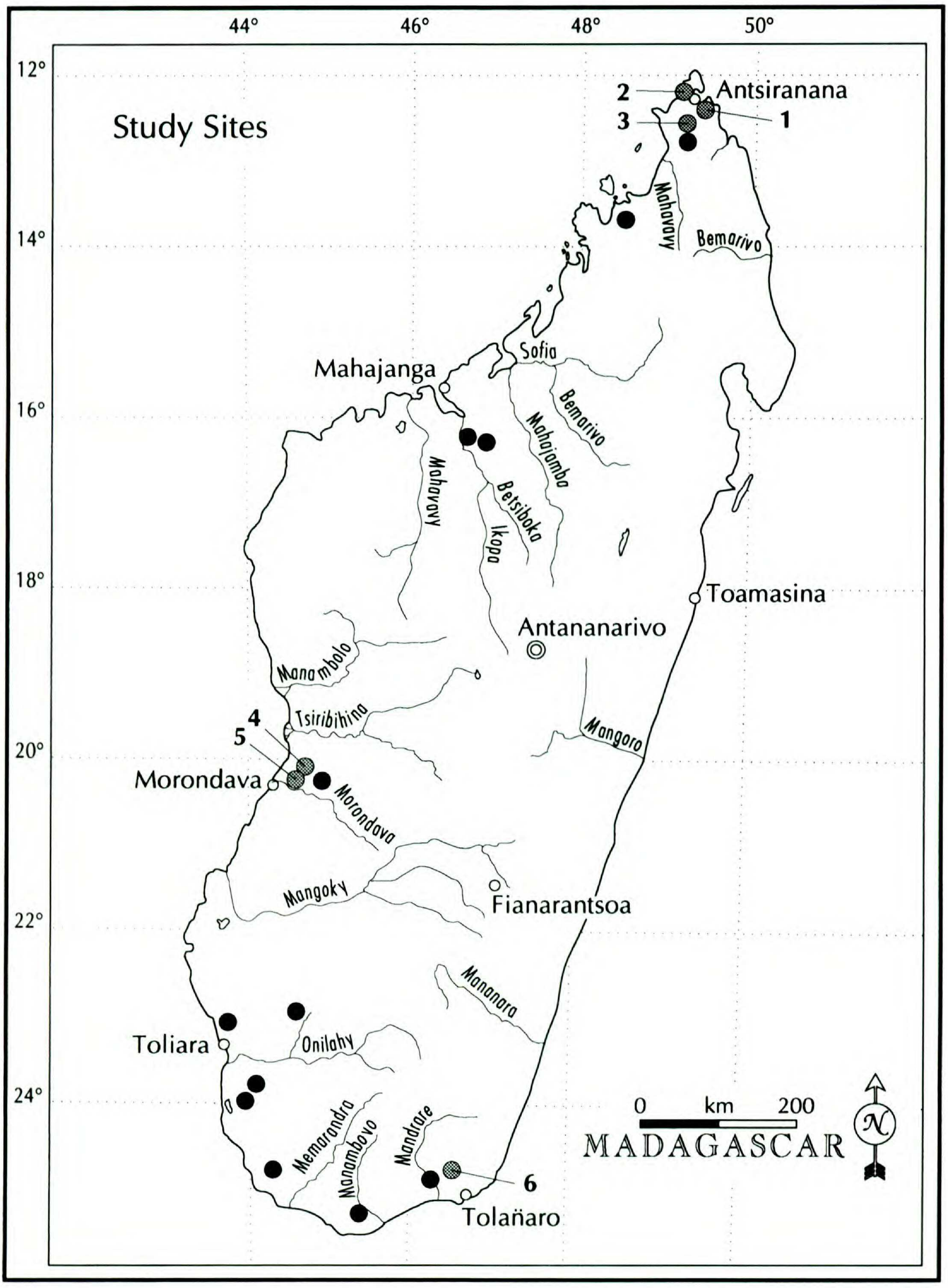


FIGURE 1. Study sites in Madagascar. Minor study sites are marked with a solid circle. Main study sites are numbered: (1) Montagnes des Français; (2) Beantely; (3) Montagne d'Ambre; (4) Kirindy Forest; (5) Marofandelia; (6) Andohahela.

TABLE 1. Dates and study sites. All localities are in Madagascar except for *Adansonia gibbosa*, which was studied in northwestern Australia (WA). For other collection localities, see Baum 1995.

Species	Dates	Locality
A. grandidieri	3–15 July 1989	Marofandelia near Morondava
A. suarezensis	6–15 June 1989	Montagnes des Français near Antisiranana
	20–22 June 1989	Beantely near Antsiranana
A. gibbosa	24 Nov.–1 Dec. 1989	Oscar ranges near Fitzroy Crossing, WA
	13–22 Dec. 1989	Meda Station near Derby, WA
	22 Dec. 1989–2 Jan. 1990	Yeeda Station near Derby, WA
A. rubrostipa	1–25 Feb. 1989	Kirindy forest near Morondava
A. madagascariensis	14–21 Mar. 1989	Montagnes de Français near Antsiranana
A. za	20–21 Dec. 1987	Andohahela near Tolagnaro (Fort-Dauphin)
	8–12 Dec. 1988	Kirindy forest near Morondava
	17–24 Dec. 1991	Kirindy forest near Morondava
A. perrieri	12–18 Nov. 1988	Montagne d'Ambre near Antsiranana
	20 Nov.–3 Dec.1991	Montagne d'Ambre near Antsiranana

Nectar concentration was measured using a temperature-compensated, hand-held refractometer (Reichert model 10431). Nectar samples, taken by letting drops of nectar dry on filter paper (Whatman #1), were analyzed by H. and I. Baker (University of California, Berkeley) for the presence of amino acids and to determine the sucrose/hexose ratio (see Baker & Baker, 1975, 1982, 1983).

In order to evaluate changes in receptivity, stigmatic morphology was examined throughout the night and day. The onset of receptivity was assessed using the peroxidase reaction. A drop of 5% hydrogen peroxide was placed on the stigma and observed with a hand-lens (magnification ×10). A positive reaction produced bubbles of oxygen. This test determines the onset of receptivity but cannot be used to detect the cessation of receptivity. In the case of *A. gibbosa*, there were significant levels of bird visitation in the early morning and it was of some importance to assess whether stigmas were receptive at that time. This was tested by emasculating buds prior to anthesis and bagging them throughout the night. These flowers were then pollinated soon after dawn with pollen from another tree in the same population. Control flowers were pollinated soon after anthesis. The fate of the flowers was followed for one month to observe whether or not abortion occurred. The breeding system experiment (see below) showed that in *A. gibbosa* most fruit abortion occurs within two weeks.

In the cases of *A. rubrostipa*, *A. madagascariensis*, *A. suarezensis*, *A. grandidieri*, and *A. gibbosa*, compatibility was assessed using pollen-tube growth. In the last species, fruit set was also measured to see if it accorded with the pollen-tube data. In both procedures, flowers were bagged during the day prior to anthesis with fine, mosquito-mesh bags. In *A. gibbosa*, the flowers were emasculated by removing the top of the calyx, opening the immature petals, and carefully cutting off all the filaments with a pair of scissors. In the other species, flowers were not emasculated. After anthesis, flowers were either selfed with pollen from the same tree or crossed with pollen from another tree.

Styles (styles and ovaries in the case of *A. gibbosa*) were collected 18 to 48 hours after pollination, fixed in 2 : 1 absolute ethanol : glacial acetic acid for 2–4 hours, and then stored in 70% ethanol. Pollen tube analysis was carried out in the laboratory of D. Mulcahy (University of Massachusetts, Amherst) using a protocol modified from Martin (1959). Styles were cleared in 8 N NaOH at 60°C for approximately 24 hr. They were rinsed in distilled water and placed in tris-glycine buffer (pH 8.4) for 15–20 min. The styles were stripped of hairs, then split longitudinally and placed with cut surfaces uppermost on a microscope slide with a drop of decolorized aniline blue (0.1% aniline blue (Allied Chemical Co.) in 0.1 M K_3PO_4). Ovaries were treated in the same way except that, after clearing, the placentas and ovules were dissected away from the ovary wall and placed on the slide. Cover slips were added and sealed with glycerin. Pollen tubes were observed using a Zeiss epifluorescence microscope at 160× and 400× magnification.

The fruit set experiment carried out on *A. gibbosa* followed the emasculation and pollination produced described above. In addition, some flowers were emasculated and bagged but left unpollinated to test for apomixis (cf. Baker, 1960). The polli-

nation bags were removed in the afternoon of the day after anthesis. Approximately two weeks later, the trees were revisited and the stage of maturation of the tagged fruit recorded.

POLLINATION

The flowers of *Adansonia* species are large, with the stigma, anthers, and nectar spatially separated. Hence, pollinators must be large-bodied and, therefore, behavioral observations and photographs were sufficient to infer whether floral visitors are likely to be major pollinators, minor pollinators, commensals, or floral parasites (see Baker et al., 1971). Observations were carried out either from the ground with binoculars or more usually from within the trees. Nocturnal observations were made using headlamps and flashlights with red filters. Photographs where taken mainly with a Pentax Super A camera and a Vivitar 80–210 mm zoom lens. At night, a small red flashlight was strapped to the lens to facilitate focusing, and a dedicated through-the-lens metered flash was used for illumination.

Animal visitors were identified in the field or from photographs. In addition, some hawkmoths were collected at flowers using a butterfly net. Malagasy specimens were deposited with B. Walther and L. Wasserthal of the Friedrich-Alexander-Universität, Erlangen-Nürnberg, Germany. Australian specimens were deposited at the Department of Entomology, Conservation and Land-management Service, South Perth, Western Australia. Hawkmoths were identified by E. Edwards, L. A. Nilsson, L. Wasserthal, and B. Walther and bats by K. Dobat.

RESULTS

FLORAL BIOLOGY

(1) Morphology. Morphological features are compared in Table 2, and Figure 2 shows a representative flower of each species. Some explanatory notes follow.

The crowns of section *Brevitubae* are distinguished from the rest of the genus by their flat-topped, "pagoda" form. The branches are tiered and more or less horizontal and the flowers are borne at the tips of orthotropic twigs. The remaining species have disorganized branches and a rounded crown.

The flowers of all *Adansonia* are borne on sturdy flower stalks comprising a proximal peduncle and a distal pedicel. The flower stalk in section *Brevitubae* and section *Longitubae* is short and either erect or more or less horizontal. In contrast, *A. digitata* (sect. *Adansonia*) has flowers that are pendulous on stalks up to 50 cm long.

Bud shape is unlikely to have any direct effect on pollination, and is probably a by-product of the development of other floral parts. In particular, petal length and width, the length of the androecium and gynoecium, and filament number are likely to affect bud shape. Baobabs have five calyx lobes, which enclose the flower completely in the bud (contrasting with the truncate calyx in all other genera of Bombacaceae). Prior to anthesis, the calyx lobes are fused along their entire length. They split apart during anthesis, curl outwards, and ultimately become twisted at the base of the flower (Fig. 2A, B, D–H). In *A. digitata* the calyx lobes reflex but do not twist (Fig. 2C). In sections *Longitubae* and *Brevitubae*, they frequently fail to separate completely resulting in a somewhat deformed flower. *Adansonia gibbosa* is unusual in the genus in that the corolla pushes through the tip of the calyx as much as 12 hours before anthesis. In the other species the corolla does not become visible until at most one hour before anthesis.

In sections *Adansonia* and *Brevitubae*, the petals and androecium more or less cover the calyx lobes in the open flower (Fig. 2A–C). In section *Longitubae*, the long staminal tube and upright petals cause the inner surface of the calyx to be exposed (Fig. 2D–H). In *A. gibbosa* this surface is cream-colored and villose like that of sections *Brevitubae* and *Adansonia* (Fig. 2A–D). In contrast, the inner calyx of *A. rubrostipa*, *A. madagascariensis*, and *A. za* is dark red (Fig. 2E–G). *Adansonia perrieri* shows intraspecific variation, with individual trees having the inner surface of the calyx pink or whitish.

Nectar is produced by a ring of calyx tissue around the base of the ovary. In *A. digitata*, the calyx tube is more or less flat and the nectar accumulates in drops on its hairy, inner (adaxial)

→

FIGURE 2. Comparison of the flowers of *Adansonia* species. The photographs show approximate relative sizes: see Table 2 for actual dimensions.—A. *A. grandidieri.*—B. *A. suarezensis.*—C. *A. digitata.*—D. *A. gibbosa.*—E. *A. rubrostipa.*—F. *A. madagascariensis* (red-petaled individual).—G. *A. za.*—H. *A. perrieri* (individual with whitish inner calyx).

TABLE 2. The floral biology of *Adansonia*.

Character	Section *Brevitubae*		Section *Adansonia*	Section *Longitubae*				
	A. grandidieri	*A. suarezensis*	*A. digitata*	*A. gibbosa*	*A. rubrostipa*	*A. madagas-cariensis*	*A. za*	*A. perrieri*
Morphology								
Crown form	flat-topped	flat-topped	rounded	rounded	rounded	rounded	rounded	rounded
Bud shape	ovoid	ovoid	globose	cylindrical	cylindrical	cylindrical	cylindrical	cylindrical
Bud length	8–10 cm	ca. 8 cm	4–7 cm	10–15 cm	24–29 cm	12–18 cm	15–22 cm	ca. 20 cm
Flower orientation	erect	erect	pendent	erect	± horizontal	± erect	± horizontal	± erect
Calyx color—outside	brown	green	green	green	green	green	green	green
Calyx color—inside	cream	cream	cream	cream	red	red	red	red or cream
Calyx tube shape	cup-shaped	cup-shaped	flat	cylinder	cylinder	cylinder	cylinder	cylinder
Calyx length vs. corolla	longer	longer	longer	shorter	longer	longer	longer	longer
Annular nectar chamber	absent	absent	absent	weak	weak	distinct	distinct	weak
Petal color	white	white	white	white	yellow	dark red	yellow	yellow
Petal shape	linear	linear	obovoid	oblanceolate	linear	linear	linear	oblanceolate
Petal widest point	above mid.	above mid.	above mid.	above mid.	below mid.	below mid.	below mid.	above mid.
Petals vs. androecium	longer	± equal	longer	longer	shorter	longer	longer	longer
Petal length	9–10 cm	8–10 cm	8–12 cm	10–15 cm	12–16 cm	12–18 cm	14–20 cm	15–24 cm
Petal length : width	ca. 5 : 1	ca. 5 : 1	ca. 1 : 1	ca. 5 : 1	>10 : 1	>10 : 1	>10 : 1	ca. 5 : 1
Staminal tube length	8–10 mm	9–12 mm	30–50 mm	25–50 mm	60–90 mm	50–90 mm	50–80 mm	130–190 mm
Free filament length	35–65 mm	50–75 mm	30–50 mm	20–80 mm	70–140 mm	50–110 mm	50–120 mm	10–20 mm
Central bundle present	no	no	no	no	yes	no	no	no
Free filament number	600–700	800–1100	720–1600	150–350	120–160	90–100	100–150	200–250
Anther size	large	large	large	small	small	small	small	small
Style color	white	white	white	white	red	red	red	pink/red

TABLE 2. Continued.

Character	Section *Brevitubae*		Section *Adansonia*	Section *Longitubae*				
	A. grandidieri	*A. suarezensis*	*A. digitata*	*A. gibbosa*	*A. rubrostipa*	*A. madagascariensis*	*A. za*	*A. perrieri*
Style shape	± straight	± straight	bent	straight	straight	± straight	straight	± straight
Stigma color	pale pink	white	white	white	red	red	red	red
Ovule number	ca. 300	?	?	350–600	ca. 300	?	?	?
Phenology								
Flowering season	June–Aug.	May–June	Nov.–Dec.	Nov.–Jan.	Feb.–Mar.	Mar.–Apr.	Nov.–Jan.	Nov.–Dec.
Flowering when in leaf	no	no	usually	usually	yes	yes	yes	young leaves
Peak number of flowers/night	40–80	30–50	10–50	10–40	10–20	20–30	20–30	10–20
Morphological Development								
Time of anthesis	1750–1820	1630–1745	1930–2000	1930–2130	1915–2115	1730–1900	1830–1945	1730–1900
Time to open (min.)	10–20	20–60	10–20	20–30	0.5–2	5–10	1–3	15–30
Flower persistence	2.5–4 days	0.5–3 days	1 day	2–4 days	1.5–3 days	3–4 days	1 day	2–3 days
Style persistent	yes	yes	yes	yes	no	no	yes	no
Calyx persistent	yes	yes	yes	yes	no	no	no	usually
Nectar								
Maximum volume (μl)	1400–1730	ca. 1900	?	64–180	59–105	250–620	200–250	150–200
Concentration (%)	13.5–18.25	11.75–12	?	17–23.5	13–15.75	?	21–22	14.5–15.25
Sucrose : hexose (n)	?	?	0.53–1.38 (4)	?	?	0.77–1.92 (4)	0.36–1.13 (12)	?
Scent								
Description	sour	sour	sour/musky	sweet	sweet	sweet	sweet	sweet

surface and on the petals. In section *Brevitubae* the nectar accumulates in an open, cuplike depression up to 1.5 cm deep. In section *Longitubae* the calyx tube fits tightly around the bases of the petals, restricting access to the nectar. In two species of *Longitubae*, *A. za* and *A. madagascariensis*, this calyx tube may have a distinct annular nectar chamber (Fig. 2G).

The corolla of *Adansonia* is composed of 5 (rarely 4 or 6) free petals attached to the base of the androecium. The petals vary in shape (see Table 2) and usually overlap for part of their length. Section *Brevitubae* tends to have relatively narrow (but sturdy) petal bases with large gaps in between, providing easy access to the nectar. In *Longitubae*, there are smaller gaps and a greater degree of overlap, hence it is more difficult to extract nectar. However, the lower parts of the petals overlap in a convolute pattern forming a cone below. The smooth inner surface of the petals would, thus, direct a flexible proboscis to one of the five angled entry points of the nectar chamber, one between each pair of petals.

In section *Brevitubae* the petals are reflexed, clasping the calyx, and are almost obscured by the spreading androecium (Fig. 2A, B). In contrast, *A. digitata* (sect. *Adansonia*) has very broad petals, which play an important role in visual display (Fig. 2C). The upper (abaxial) surface of the petals accumulates drops of nectar dislodged from the calyx. In section *Longitubae* the petals also play an important role in visual display. The flowers of *A. gibbosa* are white, becoming cream or yellow with senescence (Fig. 2D), while in *A. rubrostipa*, *A. za*, *A. perrieri*, and some *A. madagascariensis* the petals are yellow (Fig. 2E, G, H), often with a diffuse reddish streak on the adaxial surface in *A. za*. Most populations of *A. madagascariensis* have dark red petals, which provide a striking contrast to the pale androecium (Fig. 2F).

The androecium comprises a staminal tube surmounted by numerous free filaments (I will refer to the free portions of the androecium as "filaments" while recognizing that the staminal tube is probably also derived from filament tissue). In all species of *Adansonia* the androecium is white or pale yellow (tending to darken with age), and more or less glabrous. There is considerable variation in androecial form in the genus. As the name of the section suggests, *Brevitubae* have very short staminal tubes that do not significantly exceed the top of the ovary and whose width exceeds their length. Sections *Adansonia* and *Longitubae* have tubes at least twice as long as the ovary. In section *Longitubae*, except *A. perrieri*, the tubes are significantly shorter than the filaments, whereas in *A. digitata* (sect. *Adansonia*) and *A. perrieri* (sect. *Longitubae*) they slightly or greatly (respectively) exceed the length of the filaments (see Table 2, Fig. 2H).

The number of filaments is significantly higher in sections *Brevitubae* and *Adansonia* than in *Longitubae* (Table 2). Since the anthers of *Longitubae* are smaller, and there is no clear difference in ovule number among the sections, sections *Brevitubae* and *Adansonia* presumably have a higher pollen : ovule ratio.

The positioning and length of the filaments affect the distribution of the anthers. In *Brevitubae* the outer filaments are slightly longer than the inner and they spread horizontally over the top of the calyx cup (Fig. 2A, B). In *A. digitata* (sect. *Adansonia*), the relatively short filaments spread out from the top of the staminal tube forming a complete sphere, ovoid, or disc (Fig. 2C). In *Longitubae* (except *A. perrieri*) the long, free filaments form a funnel; however, there are modifications of this basic structure. In *A. gibbosa* the inner filaments are shorter than the outer, while the reverse is true of *A. rubrostipa*, *A. madagascariensis*, and *A. za*. *Adansonia rubrostipa* is unique in the genus in having a secondary staminal tube. This "inner bundle" comprises 10–15 central filaments that are fused for about 8 cm above the top of the primary staminal tube (Figs. 12, 14). This inner bundle concentrates the anthers at the center of the flower around the style. The androecium of *A. perrieri* is unique in *Longitubae*, comprising a long, slender staminal tube surmounted by short filaments, which spread out in all directions, as in *A. digitata* (Fig. 2H).

The anthers have a single, long, sinuous pollen sac running around the edge of the connective. In sections *Brevitubae* and *Adansonia* the insertion of the filament is subbasal and non-versatile, whereas in *Longitubae* it is more or less central and somewhat versatile.

The gynoecium consists of a syncarpous ovary and a single terminal style. The ovary and the lower region of the style have a dense indumentum of sharp, upward-pointing hairs up to 2 mm long. The shape of the ovary varies slightly, showing a general correlation with the shape of the mature fruit, but this does not appear to be of any significance for pollination. In contrast, style color, length, and shape are potentially important.

The style of sections *Brevitubae* and *Adansonia* and *A. gibbosa* in section *Longitubae* is white (Fig. 2A–D), while that of *A. rubrostipa*, *A. madagascariensis*, *A. za*, and *A. perrieri* is red or pink

(Fig. 2E–H). The styles of *A. grandidieri* (sect. *Brevitubae*) and *A. madagascariensis* (sect. *Longitubae*) are sometimes longer than the calyx and corolla and then they are slightly bent in the bud. More extreme is *A. digitata* (sect. *Adansonia*) with a long style that is usually bent over at approximately right angles in the globose bud (Fig. 2C). Baker (1985) suggested that the bent style of *A. digitata* might be an adaptation for bringing the stigma close to the base of the flower where it is more likely to be touched by a visiting bat. However, the possibility that this character is a developmental by-product of constraining a long style inside a bud needs to be considered. The styles of section *Brevitubae* and section *Adansonia* are sturdier than those in section *Longitubae*.

In sections *Adansonia* and *Longitubae* the stigmas, when fully open, are composed of 5–10 lobes. In *A. digitata*, and to some extent *A. gibbosa* and *A. perrieri*, the lobes are well defined whereas in *A. rubrostipa*, *A. za*, and *A. madagascariensis* they are irregular and poorly defined. In section *Brevitubae*, *A. suarezensis* has a yellowish, club-shaped stigma with no discernible lobes, whereas *A. grandidieri* has a small, irregular, pinkish stigma.

(2) Phenology. *Adansonia digitata* usually flowers at the start of the wet season (the timing of which varies across Africa), but there are many populations that flower at other times of the year (Wickens, 1983). Those introduced into Madagascar flower in November, the beginning of the wet season. Both species of section *Brevitubae* flower during the dry season (May to September). All section *Longitubae* flower during the wet season (November to March): *A. gibbosa*, *A. za*, and *A. perrieri* at the beginning of the season (November to January); *A. rubrostipa* in the middle (February to early March); and *A. madagascariensis* at the end (March to April). It is noticeable that all known Malagasy populations comprising more than one baobab species have staggered flowering with no two species overlapping. This pattern suggests character-displacement (e.g., Gentry, 1974), but such a hypothesis is difficult to evaluate.

In all the species examined, flowering phenology fits a modified steady-state pattern (Gentry, 1974; Hopkins, 1984). Flowering extends over approximately four to six weeks with relatively few flowers per night. Sections *Adansonia* and *Longitubae* appeared to produce fewer flowers per night (1–30/tree) than *Brevitubae* (30–80/tree), but further work in other localities would be useful to confirm this.

For *A. rubrostipa* (sect. *Longitubae*), the mean number of flowers open on a given night during the peak of the flowering season was 0.88 per tree. Of those trees producing flowers on a given night, the mean was 2.96 flowers. Only 5 of 25 trees averaged more than one flower per night for the 15 days on which observations were made. The highest number of flowers opening on one night on a single tree was 27, and this same individual also had the highest mean number of flowers (4.81/night). Four of the 25 trees produced no flowers during the 15 days of observation and 13 produced 5 or fewer.

(3) Floral development. *Adansonia* flowers develop in the axils of leaves or bracts, usually at the tips of branches. The very young buds of all the species studied in sections *Longitubae* and *Brevitubae* are ovoid. Buds in section *Brevitubae* retain this shape, while those of section *Longitubae* grow in length more than width, becoming elongated and cylindrical when mature. The bud growth of *A. digitata* (sect. *Adansonia*) was not examined.

On the day of anthesis, floral buds grow quickly (as much as 4 mm/hr. in *A. rubrostipa*) and generally become paler. In all species studied, pollen is released in the bud approximately 2–6 hours before anthesis. A minimal amount of nectar also accumulates.

Anthesis, here defined as the opening of the flower bud from the earliest splitting of the calyx until the lobes are fully free and twisted at the base of the flower, takes place in the evening in all species of *Adansonia*. In *A. suarezensis* (*Brevitubae*) and *A. madagascariensis* (*Longitubae*) anthesis commences before dark, as early as 1630h in the former case (sunset at approximately 1730h) and 1730h in the latter (sunset at approximately 1800h). The other species all undergo anthesis after dark, usually within an hour of dusk (up to 2.5 hr. in *A. rubrostipa*).

The flowers of a tree are generally well synchronized, all opening within an hour of each other. The synchronization between trees is weaker, with opening spread out over as much as 2.5 hr. In the case of *A. rubrostipa*, individual trees could generally be characterized as either late or early openers. It is not known whether intrinsic (circadian) or external cues determine the time of anthesis.

Adansonia species fall into two groups with respect to the rate anthesis (Table 2). In *A. grandidieri*, *A. suarezensis*, *A. digitata*, *A. gibbosa*, and *A. perrieri* anthesis takes from 10 to 60 minutes, the slowest being the day-opening *A. suarezensis*. In *A. rubrostipa*, *A. madagascariensis*,

and *A. za* anthesis is spectacularly rapid, being easily followed with the naked eye. The buds (15 to 29 cm long) usually take only 2–3 minutes to open, but sometimes as little as 30 seconds in *A. rubrostipa*. The cellular basis of the rapid anthesis is unknown. However, the outer layer of the calyx is rigid and growth or cell expansion in the inner layer could be responsible for the movements of the lobes during anthesis.

At the end of anthesis (as defined here), the calyx is loosely coiled at the base of the flower and the petals and androecium are partially expanded. During the next few hours the coiling of the calyx becomes progressively tighter and the filaments gradually spread outwards. However, this intensified turgor lasts only about 6 hours, after which the floral parts become more flaccid.

Three of the species studied (*A. suarezensis*, *A. digitata*, and *A. za*) had flowers that usually abscised within 24 hours of anthesis. In all three, the styles persist after the corolla and androecium have abscised (presumably to allow for the completion of pollen-tube growth). The other species had flowers lasting two to four days and of these *A. rubrostipa*, *A. madagascariensis*, and *A. perrieri* have caducous styles that fall attached to the androecium.

The calyx is persistent in section *Brevitubae*, *A. digitata* and *A. gibbosa*, whereas in *A. rubrostipa*, *A. madagascariensis*, and *A. za* it is caducous with a well-defined abscission zone close to its base. *Adansonia perrieri* is variable, in that the calyx is usually caducous but sometimes somewhat persistent.

(4) Scent. In sections *Brevitubae* and *Adansonia* the flowers have a sour, none-too-pleasant smell. The closest description I can give of the odor of *A. grandidieri* is "sour watermelon." Flowers of section *Longitubae*, in contrast, have a sweet, pleasant fragrance. In *A. gibbosa* the scent is heavy and reminiscent of vanilla. In the others it is lighter and more gardenia-like.

(5) Nectar. Comparative nectar data are presented in Table 2. Quantitative measurements of nectar volume were not made on *A. digitata*, but I observed large droplets of nectar on the inner surface of the calyx and estimate that at least 500 μl is produced by this species. Hence, it appears that the total volume of nectar produced by sections *Adansonia* and *Brevitubae* is much higher than in section *Longitubae*.

The course of nectar production was studied in more detail in *A. grandidieri*, *A. gibbosa*, *A. za*, *A. perrieri*, and *A. rubrostipa* (Figs. 3, 4).

In *A. grandidieri*, nectar production started at anthesis and continued at a fairly constant rate (approximately 110 μl/hr.) throughout the night, slowing around dawn (52–75 μl/hr.). It was not determined when nectar flow ceased. Despite some variability, it appears that *A. za* (Fig. 4A) and *A. gibbosa* (Fig. 3C) produce nectar constantly throughout the night, but at a much slower rate than *A. grandidieri* (Fig. 3A; note the scale of the y-axis). Two of the *A. gibbosa* trees studied and the single *A. za* appeared to show nectar resorption soon after dawn, but the effects of sampling error cannot be ruled out.

Although sparse, the data for *A. rubrostipa* suggested that most of the nectar is produced before and soon after anthesis (Fig. 3E), whereas in *A. perrieri* it occurs between 2100h and 0300h (Fig. 4C). However, the low nectar production by *A. rubrostipa* during the night could be an artifact caused by progressive damage to the nectariferous tissue during nectar extraction.

Nectar concentration data are summarized in Table 2. The nectar concentration of section *Brevitubae* (ranging from 11.75 to 18.25%) is within the range of known bat-pollinated taxa (e.g., 11.75 to 15.4%, Ramirez et al., 1984; 26.6 ± 1.5% and 27.2 ± 1.9%, Kress, 1985). In *Longitubae*, *A. za* (19 to 22%) and the Australian species *A. gibbosa* have a nectar concentration similar to the average of 22.1% for hawkmoth-pollinated plants reported by Pyke & Waser (1981). The other Malagasy *Longitubae* (*A. rubrostipa*, *A. perrieri*, and *A. madagascariensis*), with a range of 13 to 18.5%, have more dilute nectars similar to the mean of 13.3% reported for a Malagasy sphingophilous orchid species (Nilsson et al., 1985, 1987).

Figures 3 and 4 also summarize the changes in the nectar concentration throughout the night for *A. grandidieri*, *A. gibbosa*, *A. rubrostipa*, *A. perrieri*, and *A. za*. Four of the five *A. grandidieri* trees, *A. za*, and *A. perrieri* had nectar that declined slowly in concentration during the night. In *A. rubrostipa* it remained more or less constant in the few hours after anthesis but had decreased by the next morning. Changes in nectar concentration in *A. gibbosa* varied greatly between trees. However, within a tree a fairly consistent pattern was detected in which nectar concentration remained fairly constant during the night but became weaker after dawn.

The analyses of nectar composition are shown in Table 2. Sucrose:hexose ratios were variable within species but tended to be relatively rich in sucrose. *Adansonia digitata* has a mean ratio of

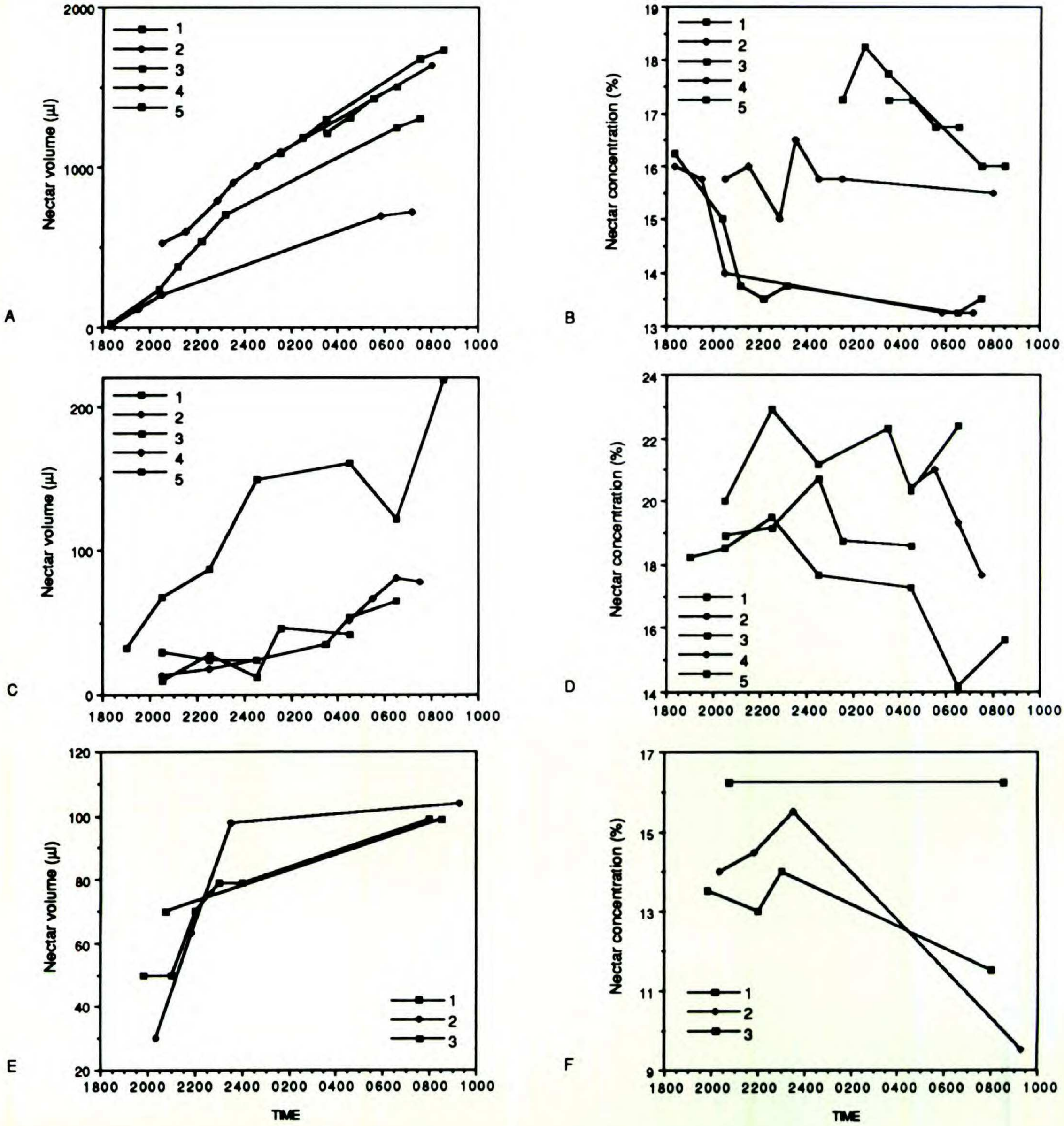


FIGURE 3. Nectar production in *Adansonia grandidieri* (A, B), *A. gibbosa* (C, D), and *A. rubrostipa* (E, F). Figures show cumulative nectar volume when repeated collections from the same flower (E) or actual nectar volume when separate flowers sampled (A, C). Nectar concentration is given in percent sucrose equivalent (B, D, F). Each point on C and D represents an average of 2–8 flowers from the same tree.

0.87, which is more sucrose-rich than for most bat-pollinated plants but not unusual for an Old World species (Baker & Baker, 1983). This value is also typical of the few non-flying-mammal pollinated plants studied (Baker & Baker, 1983).

The nectar of *A. za* had a very variable sucrose : hexose ratio ranging from 0.36 ("hexose-rich") to 1.13 ("sucrose-dominated"). The mean, however, based on 10 samples from throughout the range, was 0.68 ("sucrose-rich"; Baker & Baker, 1983). In *A. madagascariensis*, the nectar had the highest sucrose : hexose ratio of the three species studied, and with a mean of 1.38, it is sucrose-dominated. Sucrose-dominated nectar is particularly common in hawkmoth flowers, though it is also known from paleotropical bat flowers and non-flying-mammal flowers (Baker & Baker, 1983).

Overall, the sucrose : hexose ratios of *Adansonia* show no clear pattern of interspecific variation, possibly because both Old World mammals and hawkmoths (the two major pollinators, see below) favor sucrose-rich nectar.

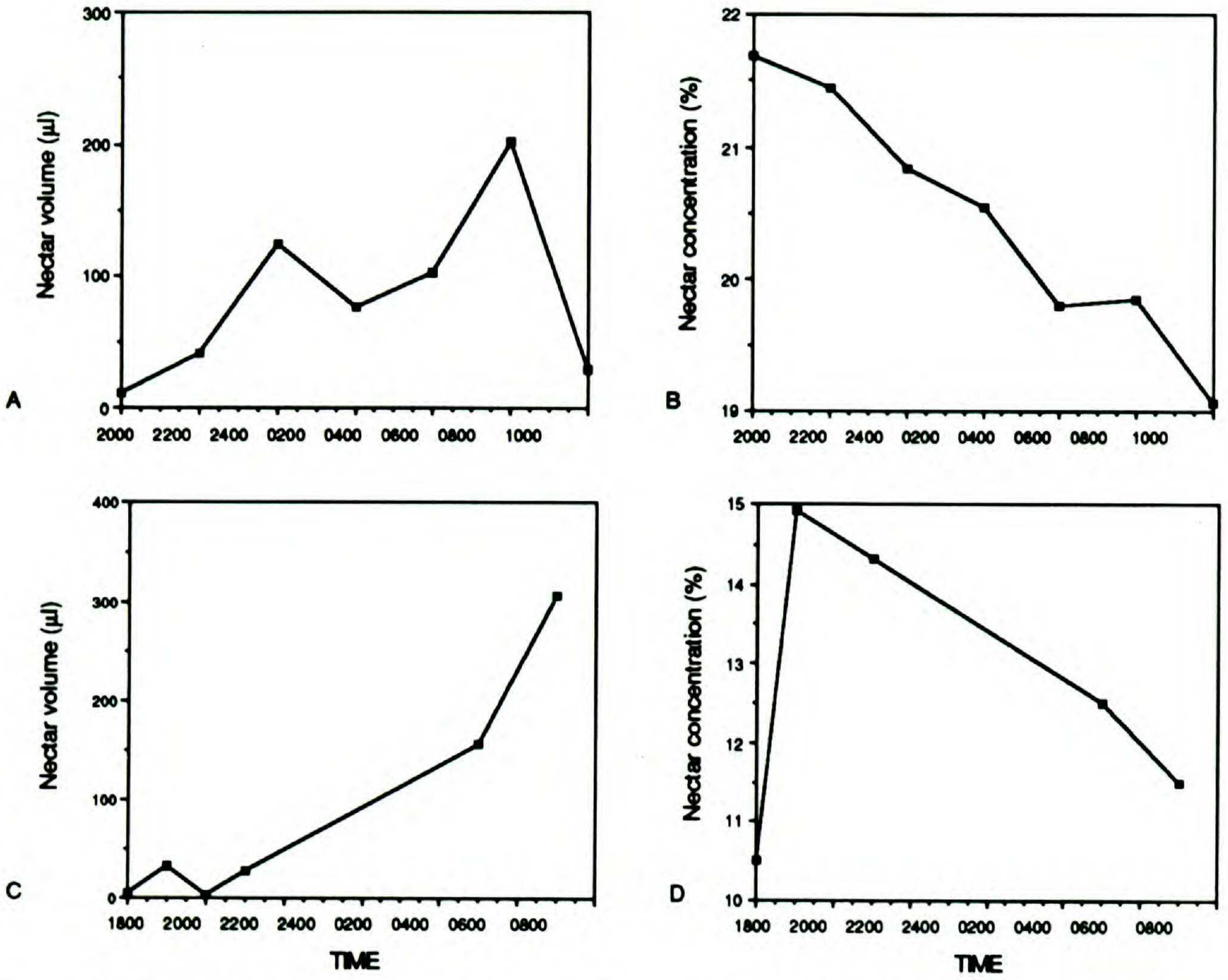


FIGURE 4. Nectar production in *Adansonia za* (A, B) and *A. perrieri* (C, D). Figures show actual nectar volume (A, C) or nectar concentration (percent sucrose equivalents; B, D) plotted against time. Each point represents an average of 2–5 flowers from the same tree.

In *A. za*, relatively high concentrations of amino acids (8–10 on the histidine scale) were detected (I. Baker, unpublished data). In two samples analyzed further, glutamine and asparagine were the most abundant, followed closely by serine (I. Baker, pers. comm.). The significance of these data is unclear.

(6) Stigmatic receptivity. In species with well-developed stigmatic lobes, the lobes start to expand either before or just after anthesis, having been infolded in bud. In all *Adansonia*, brown, senescent tissue appeared on the stigma by dawn or soon after. By mid-morning the stigmas are completely brown and dry (in the absence of rain). In *A. gibbosa*, the stigmatic lobes, as well as browning, often become slimy and wet between about 0200h and 0400h, drying out again later.

The peroxidase test was positive in all species either at anthesis or within an hour afterwards. As an indicator of general metabolic activity these data are consistent, with stigmatic receptivity commencing about the time of anthesis. This is further supported by the breeding system experiments (reported below) in which pollen was applied to flowers at or soon after anthesis. In all cases, these hand pollinations successfully led to pollen-tube growth, and in the case of *A. gibbosa* fruit set was also observed.

In *A. gibbosa* a hand-pollination experiment was conducted in order to determine whether stigmas remain receptive in the early morning. Of the 19 flowers pollinated during the night (13 at 2200h, 6 at 2400h), 6 (31.6%) remained attached one month after pollination, indicating successful fertilization. Of the 31 pollinated in the early morning (13 at 0400h, 6 at 0500h, 13 at 0600h), 15 (48.4%) were still attached one month later. Hence, *A. gibbosa* stigmas remain receptive into the early morning.

(7) Breeding systems. Examination of all open- or hand-pollinated styles under the microscope revealed characteristic spinulose pollen grains on the stigma. Pollen tubes were visible just below the stigma, but they were less apparent further down the style, perhaps due to differences in callose deposition (aniline blue stains callose). A few iso-

TABLE 3. Breeding experiment on *A. gibbosa*. The four trees were at the Oscar Range site. Pollinations were carried out between 2030 h and 2130 h on 24–30 Nov. 1989. The number of fruits still attached to the tree on 1 Jan. 1990 is shown. The number of flowers in each category is given in parentheses.

Tree	Number of days fruit allowed to develop	Distance to pollen donor	Number remaining (Number at start)		
			Unpollinated	Self	Cross
1	36	4.5 km	0 (10)	0 (10)	10 (10)
2	38	350 m	–	1 (10)	6 (10)
3	34	115 m	0 (5)	0 (4)	2 (5)
	32	115 m	0 (5)	0 (6)	4 (5)
4	34	8 m	0 (5)	0 (4)	4 (5)
	32	8 m	1 (5)	0 (6)	4 (5)
Totals			1 (30)	1 (40)	30 (40)

lated pollen tubes with irregular callose plugs could often be seen, however. At the very base of the style, where the conducting tissue narrows just before entry into the ovary, the pollen tubes were highly visible and often very numerous. Thus, while the poor visibility for much of the style limited the accuracy with which pollen-tube growth can be measured, the high visibility at the base of the style permitted it to be determined with confidence whether pollen tubes had successfully penetrated the ovary.

In *A. rubrostipa* and *A. madagascariensis* pollen tubes were given from 18 hr. 10 min. to 42 hr. 30 min. to grow, but none reached the bottom of the style during that time. Despite the few styles examined (five for *A. rubrostipa*, six for *A. madagascariensis*), there was no evidence that the growth of self-pollen-tubes was any less than that of cross-pollen-tubes; in fact, the self- had, on average, penetrated further than the cross-pollen-tubes. In the cases of *A. grandidieri* and *A. gibbosa*, both self- and cross-pollen-tubes grew down the entire style with no noticeable difference in rate. Of the 28 styles of *A. grandidieri* (13 selfs, 15 crosses), only one lacked pollen tubes at the base. Of the 10 styles of *A. gibbosa* (7 selfs, 3 crosses), only two lacked pollen tubes at the base. A single self-pollinated style of *A. suarezensis* was likewise observed to have pollen tubes at the base.

These data suggest that there is no inhibition of self-pollen-tube growth in the style. Furthermore, in *A. gibbosa* both cross- and self-pollen-tubes were observed entering the ovules through the micropyle. Pollen-tube growth data thus suggest self-compatibility in the *Adansonia* species studied.

In order to investigate whether the equality of pollen-tube growth resulted in equal fruit set of selfs and crosses, a hand-pollination experiment was carried out in *A. gibbosa*. Almost all the unpollinated and selfed flowers had aborted 32–38 days after anthesis (Table 3). In contrast, 75% of the cross-pollinated flowers remained attached to trees at that time. This suggests that the flowers are functionally self-incompatible. Since the pollen-tube data show that self-pollen-tubes can successfully penetrate the ovules, incompatibility must be late-acting (Cope, 1962; Seavey & Bawa, 1986). Late-acting self-incompatibility involving early abortion of fertilized ovules is known in *Chorisia* (Gibbs & Bianchi, 1993) and *Eriotheca* (Oliveira et al., 1992) also in the Bombacaceae.

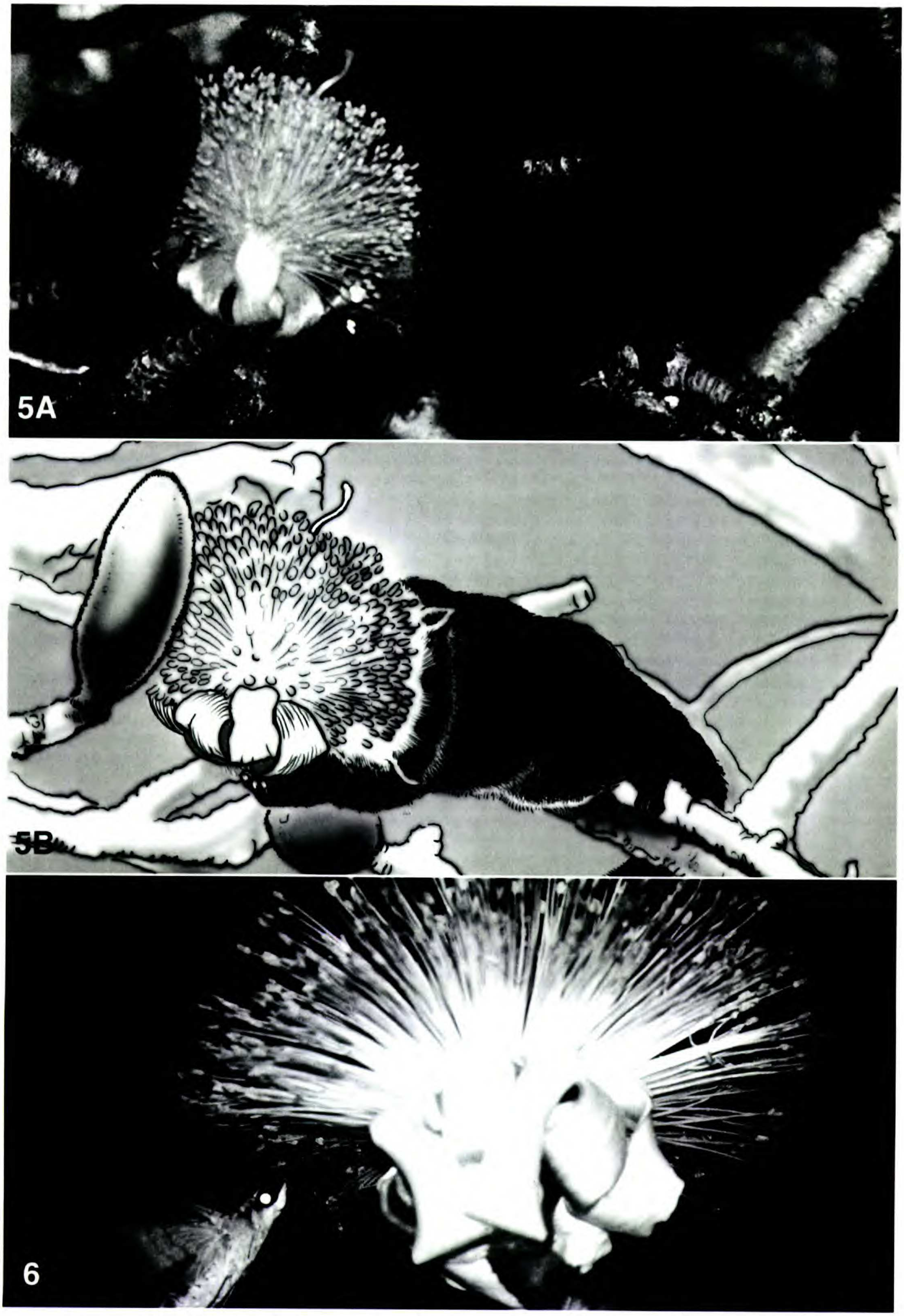
POLLINATION BIOLOGY

The results of nocturnal and diurnal floral watches for each species are described below and summarized in Table 4.

(1) Adansonia grandidieri. When observations were made in forested sites near Marofandelia, fork-marked lemurs (*Phaner furcifer* Blainville) made non-destructive visits to the flowers (Fig. 5). One or a pair of animals moved through the canopies of two adjacent baobabs visiting flowers (approx. 2 visits/flower/hr.). The animals inserted their snouts into the sides of the flowers and licked nectar from the petal bases. This behavior results

TABLE 4. The peak visitation rate of classes of floral visitors to *Adansonia* species (abbreviated to first three letters). – = no visits observed. + = 0–1 visits/fl/hr. ++ = 1–10 visits/fl/hr. +++ = >10 visits/fl/hr. Inferred major pollinators are marked with square brackets, minor or possible pollinators with parentheses.

	gra	sua	dig	gib	rub	mad	za	per
Bees, flies, butterflies	++	+++	++	+	+	(+++)	++	+
Settling moths	–	+	+	++	+++	+	+	+
Hawkmoths	++	++	+	[++]	[+++]	–	[+++]	[+++]
Birds	++	++	–	(++)	+	–	++	+
Non-flying mammals	[++]	–	(+)	–	++	–	(++)	–
Bats	–	[+]	[++]	–	–	–	–	–



FIGURES 5, 6. Floral visitors of *Adansonia grandidieri*. —5. Lemur (*Phaner furcifer*) as shown in the photograph (5A) and line drawing (5B). Note pollen deposited on the animal's face. —6. Hawkmoth (*Nephele comma*).

in pollen being deposited on the animal's face (Fig. 5). Although I was not able to see stigmatic contact, in view of the animals' large body size some pollination is likely to occur. *Phaner* is omnivorous, feeding on insects, fruits, flower-buds, flowers, and especially gums (Petter et al., 1975; Charles-Dominique & Petter, 1980). Sussman & Raven (1978) suggested a role for *Phaner* in the pollination of Malagasy plants, but this prediction has not previously been confirmed. Of the other lemur species that are sympatric with *A. grandidieri*, only one other is a confirmed nectar feeder, the dwarf lemur, *Cheirogaleus medius* E. Geoffroy (see below). However, *Cheirogaleus* hibernates during the dry season and is, therefore, not a potential pollinator of *A. grandidieri*.

Despite indications by local people that bats visit flowering *A. grandidieri* trees, no bat visits were observed during two weeks of nocturnal observations. This absence could be due to the proximity of the study site to a village and the fact that fruit bats are trapped locally for food. Additional work in some more isolated populations (e.g., near Lac Ihotry, south of Morombe) is needed to determine whether bats are pollinators of *A. grandidieri*.

In the morning after anthesis a few honeybees and small sweat bees collected pollen, but did not contact the stigmas. Since no effective pollinators visit the flowers after dawn, the bees probably have no detrimental effect and represent commensals.

Hawkmoths identified from photographs as *Nephele comma* Hopfer (L. A. Nilsson, pers. comm.) were reliable visitors in the first 30 minutes after anthesis and the 30 minutes before dawn (Fig. 6). The peak visitation rate observed was 8 visits in 20 minutes (24 visits/flower/hr.), each visit lasting 5–20 seconds. The moths approached the flowers from the side, below the level of the androecium, and thus no pollination occurred. By removing nectar that could attract legitimate pollinators, hawkmoths probably have a slight negative effect on reproductive output.

Soon after dawn, large numbers of sunbirds visited the flowers and fed on nectar and occasionally on small bees that were collecting pollen. *Nectarinia souimanga* Gmelin and *N. notata* Müller were observed with equal frequency. They perched below the flowers on the flower stalk or calyx and fed by inserting their beaks under the filaments (Fig. 7). As a result, despite the high visitation rate (5–10 visits/flower/hr.), they are responsible for little pollen transfer. In the absence of information about the flower's ability to reabsorb excess nectar, it is unclear whether the sunbirds have a net negative or neutral effect on the plant.

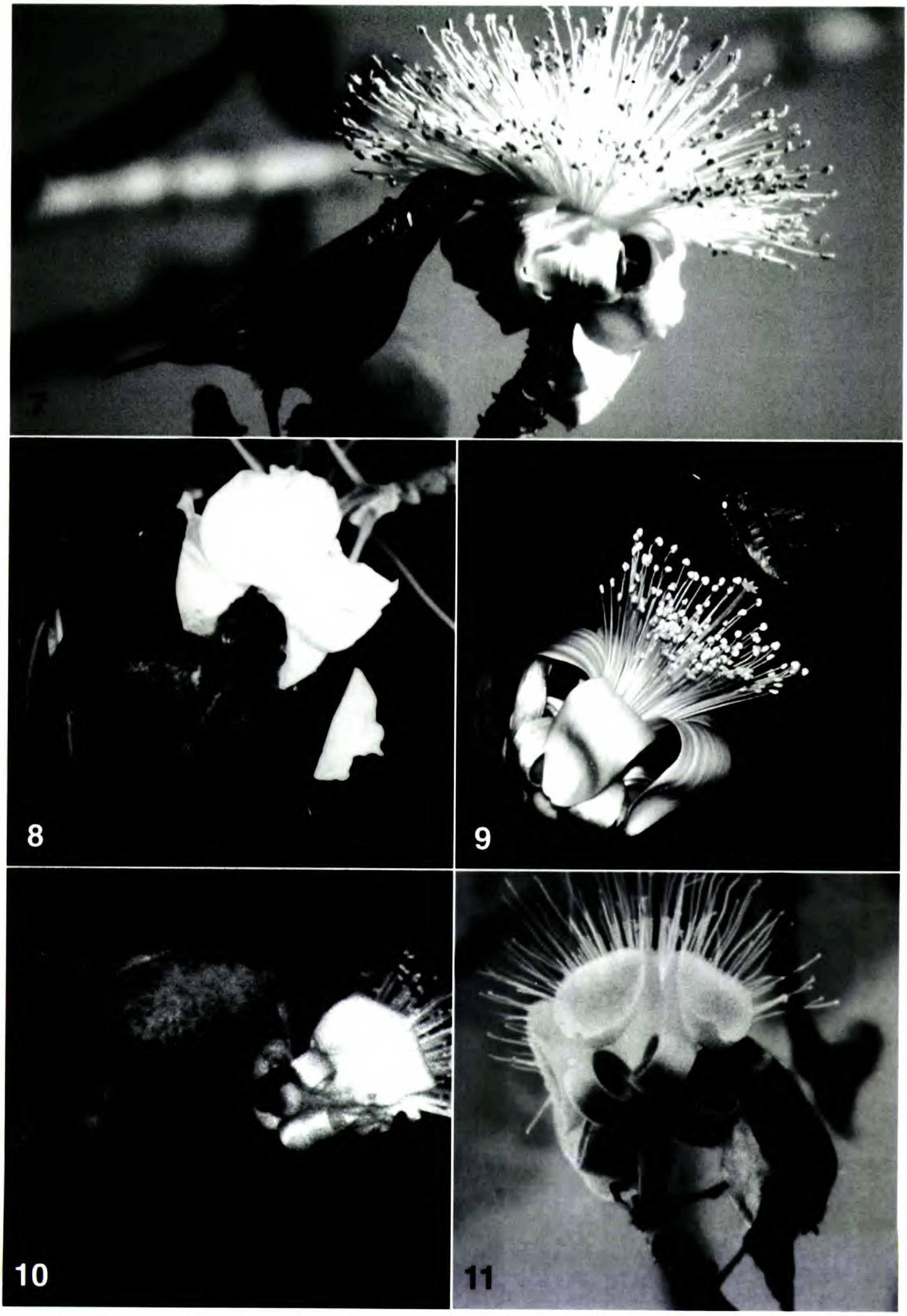
Adansonia grandidieri is clearly pollinated primarily by nocturnal mammals, but further work is needed to determine whether bats, as well as lemurs, play a role. Other floral visitors seem not to contribute significantly to pollination.

(2) Adansonia suarezensis. The first of the two study sites, the Montagne des Français on the west of the Baie d'Antsiranana, is a heavily disturbed patch of deciduous forest merging into overgrazed *Cryptostegia* (Asclepiadaceae) scrub-land. No pollinating visits were observed during more than one week of nocturnal observation. However, at the second study site, the less disturbed deciduous forest at Beantely, visits by fruit bats (probably *Eidolon dupraenum* Pollen) were observed. The visits were concentrated in the hour after dusk, but occurred at a low rate throughout the night (observations made close to full moon). Accurate visitation rates were hard to assess because my presence disturbed the bats. Fourteen visits/tree/hour (approximately 0.5 visits/flower/hr.) was the peak rate observed. The bats landed close to a flower and then clambered over to it. Each visit lasted 20–30 seconds, with as many as nine flowers being visited in succession. Usually, a bat would leave the tree immediately after completing a visit and fly to another flower on the same or another tree, but sometimes it clambered directly from one flower to another.

In view of the bats' large body size and the way they envelop the flowers when feeding, pollen transfer seems inevitable. In view of their strong flight (Heithaus et al., 1974; Faegri & van der Pijl, 1979), fruit bats are likely to cause both self- and cross-pollination. Only three species of fruit bat occur in Madagascar, *Eidolon dupraenum*, *Pteropus rufus* E. Geoffroy, and *Rousettus madagascariensis* G. Grandidier. The latter is restricted to a small area on the east coast, whereas the others occur in coastal areas throughout the island (Dorst, 1947; Sussman & Raven, 1978).

The mature buds of *A. suarezensis* start to open in the late afternoon, as much as one hour before dusk. Numerous honeybees visit the flowers between anthesis and dusk. Honeybees and sweat bees also forage on flowers early in the morning. In all cases pollen rather than nectar was collected and no contact was made with stigmas. Since the bees visit in the evening before the legitimate pollinators, they are probably detrimental to the plants' reproductive output and, thus, represent floral parasites.

During the night, visits by unidentified hawkmoths were occasionally observed. The proboscides



FIGURES 7–11. Floral visitors of *Adansonia grandidieri* (7), *A. digitata* (8), and *A. gibbosa* (9–11).—7. Sunbird (*Nectarinia notata*).—8. Fruit bat (*Roussettus aegyptiacus*).—9. Hawkmoth (*Agrius convolvuli*).—10. Little friarbird (*Philemon citreogularis*).—11. Singing honeyeater (*Lichenostomus virescens*).

were less than 5 cm in length, and the approach was exclusively from below the flower in the same manner as in Figure 6. Thus, these visits did not result in pollination.

Soon after dawn, souimanga sunbirds (*Nectarinia souimanga*), visited the flowers that had opened the evening before. Their behavior was the same as that of the sunbirds that visited *A. grandidieri* (Fig. 7); they perched on the flower stalk or calyx and inserted their beaks underneath the filaments into the cup-shaped nectar chamber. As many as five visits per flower in the first hour after dawn were observed, each lasting from 5 to 60 seconds. During longer visits the birds removed and reinserted their beaks several times from different positions around the periphery of the flower. Despite the regularity of the visits, the sunbirds did not contribute to pollination because of the great distance between the nectar chamber and the stigma. Sunbirds are thus acting as nectar thieves, but since their visits occur after those of the legitimate pollinators and do not visibly make contact with the gynoecium, they will only have a detrimental effect on baobab fitness if the plants can reabsorb excess nectar.

My observations suggest that *A. suarezensis* is primarily pollinated by fruit bats. Although I observed no visits by lemurs, they cannot be ruled out as secondary pollinators in other forests. Birds and insects, although frequent visitors, do not contribute significantly to pollination.

(3) Adansonia digitata. In view of the existing literature (reviewed in Wickens, 1983; Dobat & Peikart-Holle, 1985), little time was spent working on *A. digitata.* However, some nocturnal observations in Kenya confirmed that fruit bats (*Rousettus aegyptiacus*) were frequent visitors, especially in the first two hours after anthesis. They were observed landing on the pendent flowers and licking nectar from between the petal bases (Fig. 8). The visits lasted five to ten seconds, and contact with the anthers and stigma was clearly observed.

(4) Adansonia gibbosa. Hawkmoth visits were not observed until the beginning of January, by which time most baobabs had finished flowering. The only hawkmoth visitor seen was *Agrius convolvuli* L. (Fig. 9). Visits were concentrated in the first half-hour after anthesis and reached a peak rate of approximately 5 visits/flower/hr. The moths hovered in front of the flowers for 3–5 seconds, inserting their proboscides, which are ca. 9 cm long, through the filaments, down to the base of the flower. In the process, they came into contact with both the anthers and stigma and were clearly efficient pollinators.

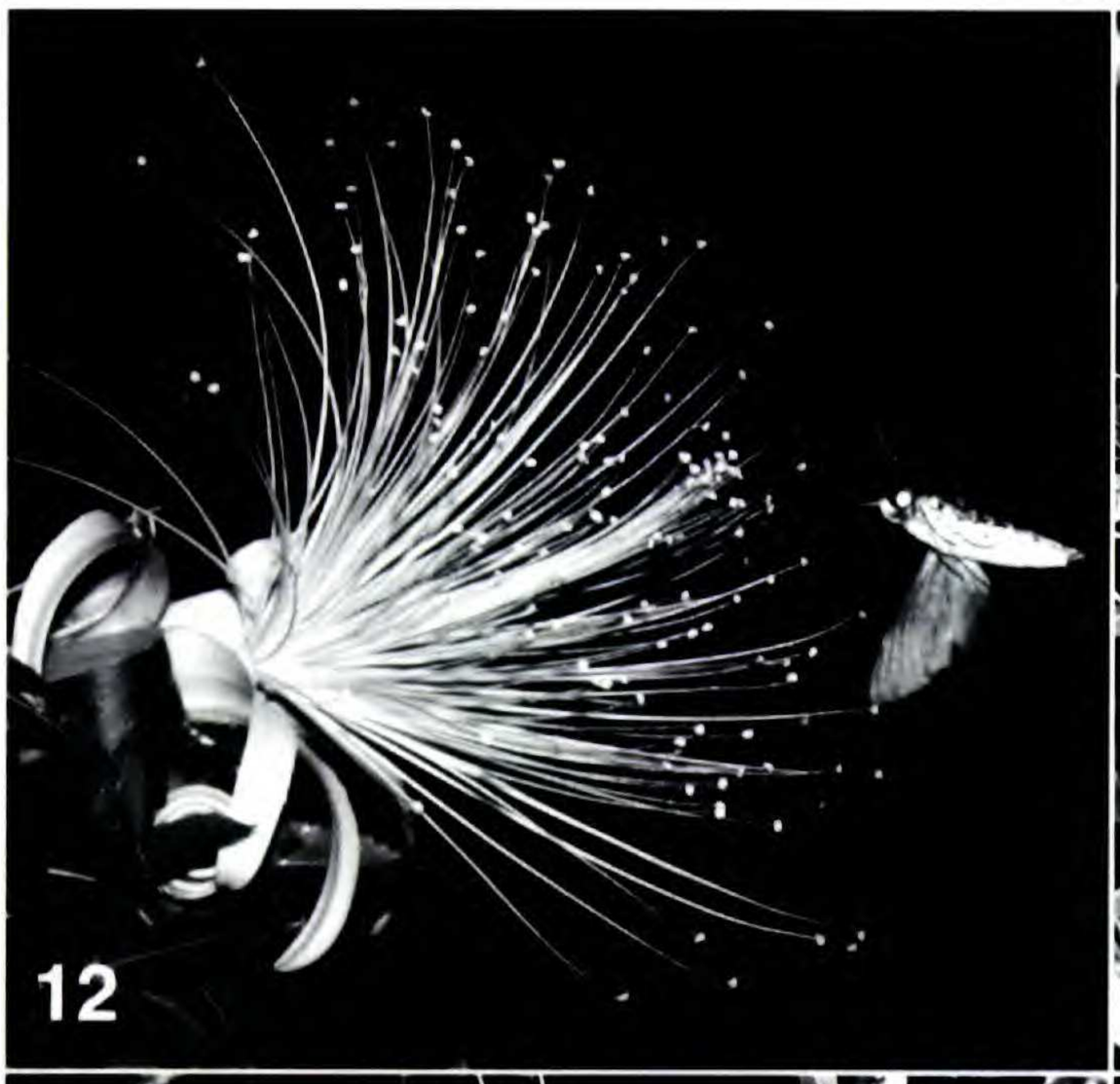
The lack of phenological synchronization between the hawkmoths and baobabs is problematic if hawkmoths are the major pollinators of *A. gibbosa.* Two alternative hypotheses could account for this seasonal discrepancy. Firstly, in highly seasonal climates, lack of synchronization is almost certain to occur occasionally because plants and their pollinators are unlikely to be utilizing exactly the same seasonal cues. Thus, unusual seasons in the study year could, by chance, have resulted in hawkmoth emergence after baobab flowering. Secondly, a hawkmoth species emerging earlier than *Agrius convolvuli* might be the major pollinator of *A. gibbosa,* and this sphingid species might have had a poor season in 1989/1990. Thus, given the lack of any other effective pollinators (see below) and the evidence of self-incompatibility in *A. gibbosa,* hawkmoths are almost certainly the main pollinators, despite the few visits actually observed.

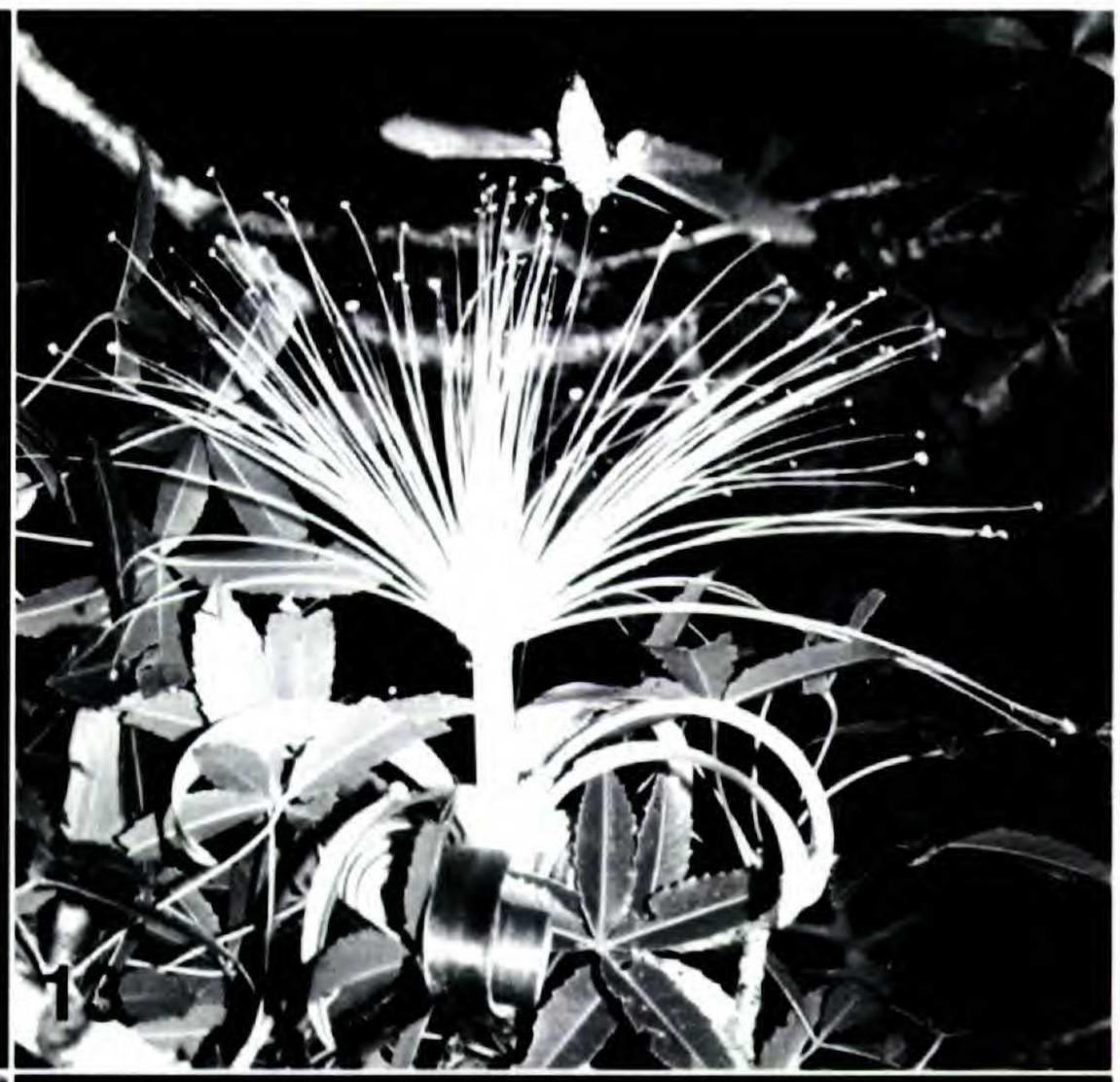
The flowers of *A. gibbosa* were visited by bees collecting pollen in the early morning and by settling moths extracting nectar at night. However, since neither of these flower visitors contacted the stigma, they did not contribute to pollination.

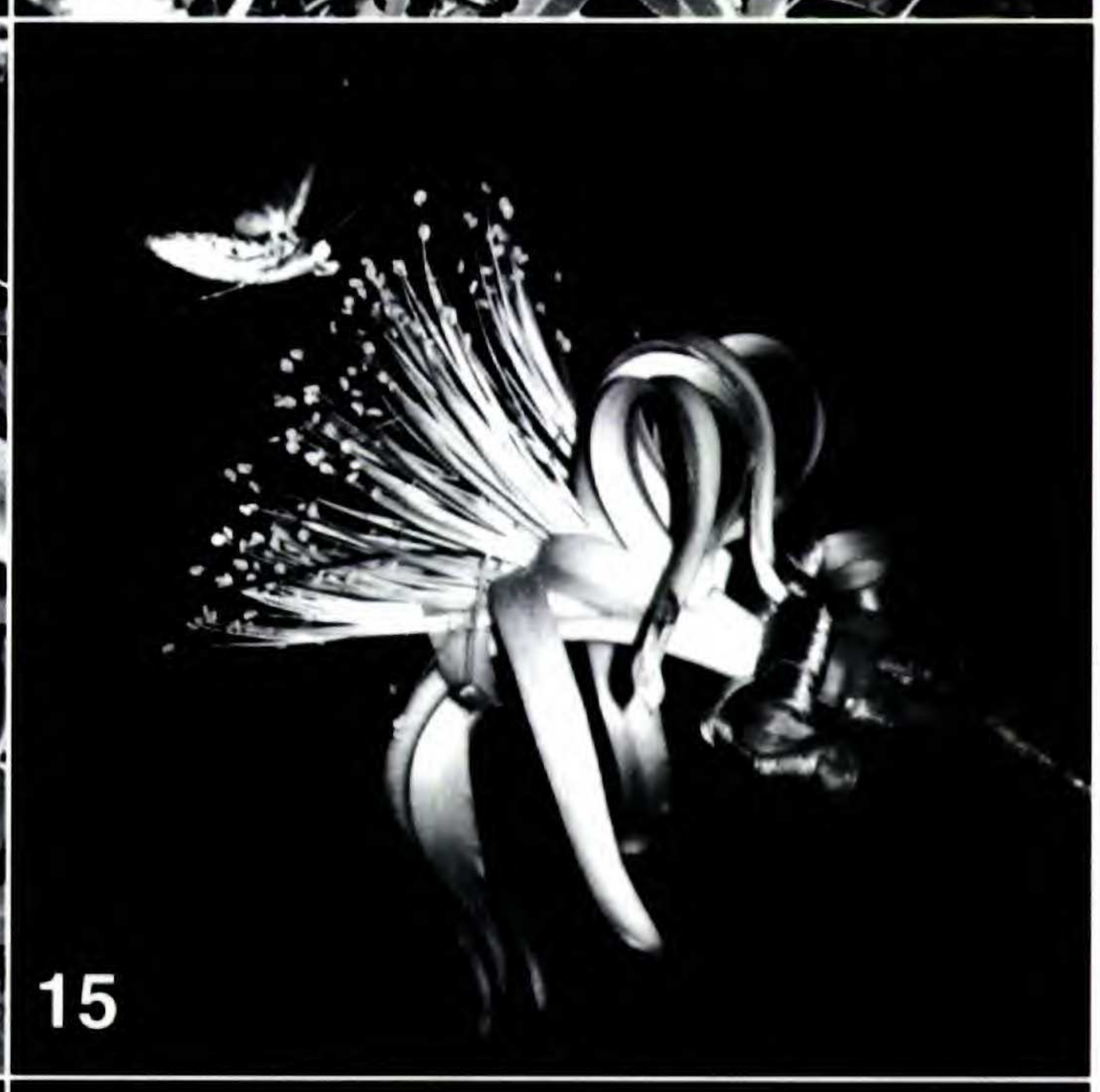
Bat visits were not observed, despite extensive nocturnal observation throughout the range of *A. gibbosa.* However, the blossom bat, *Macroglossus* sp., has been trapped in the vicinity of flowering baobabs (K. Kenneally, pers. com.). Also, van der Pijl (1956) reported claw marks on *A. gibbosa* petals in Java, which he interpreted as being caused by bats. Based on this circumstantial evidence, it is conceivable that bats might occasionally visit the flowers, but they are unlikely to be major pollinators of *A. gibbosa.*

Bird visits were frequent in the early morning (0430–0530h), and occasional at other times of day. Honeyeaters (family Meliphagidae) were the most important (Figs. 10, 11), especially yellow-throated miners (*Manorina flavigula* Gould), little friarbirds (*Philemon citreogularis* Gould), and brown honeyeaters (*Lichmera indistincta* Vig. & Horsf.). Other honeyeaters that visited flowers included: singing honeyeaters (*Lichenostomus virescens* Vieillot), gray-fronted honeyeaters (*Lichenostomus plumulus* Gould), and banded honeyeaters (*Certhyonix pectoralis* Gould), in addition to yellow white-eyes (*Zosterops lutea* Gould) and red-collared lorikeets (*Trichoglossus rubritorquis* Vig. & Horsf.). All these species were primarily nectar feeders. The peak visitation rate was 8 visits/flower/hr., but was usually much lower.

During nectar-foraging the birds perched on the peduncle or calyx, and inserted their beaks into the bases of the flower (Figs. 10, 11). In this position, little if any pollen is applied to the birds







FIGURES 12–17. Floral visitors to *Adansonia rubrostipa* (12–14), *A. za* (15), and *A. perrieri* (16, 17).—12, 13. Hawkmoth (*Coelonia solanii*).—14. Lemur (*Cheirogaleus medius*).—15. Hawkmoth (*Coelonia solanii*).—16. Hawkmoth (*Coelonia solanii*).—17. Hawkmoth (*Xanthopan morgani*).

and no stigmatic contact occurs. In less than 5% of cases birds visited flowers from an adjacent branch, and in this position they could make contact with the stigma. Since flowers are receptive in the early morning (see above) birds might contribute to pollen transfer in *A. gibbosa*, but whether this offsets the detrimental effect of bird foraging (e.g., damage to flowers and/or removal of nectar otherwise destined for reabsorption) remains to be assessed.

(5) Adansonia rubrostipa. The flowers of *A. rubrostipa* were visited throughout the night by the long-tongued hawkmoth, *Coelonia solanii* Boisduval, with a peak of activity soon after anthesis. The visitation rate differed markedly between trees, the highest being 18 visits/flower/hr.

Coelonia approached the flowers from the front, extending their proboscides when about 10 cm away from the flower. The proboscis was inserted through the central filaments (Figs. 12, 13) down to the base of the flower, presumably passing between the petals at their bases and thereby entering the nectar cavity. The moths usually engaged in brief upward and downward movements during the insertion of the proboscis, similar to those described by Brantjes & Bos (1980). However, "swing-hovering" described in *Coelonia solanii* and other Malagasy sphingids (Wasserthal, 1993) was not observed. Visits usually lasted 2–5 seconds, rarely up to 20 seconds, and pollen was scattered on the moths' wings and bodies. Contact with the dark red style and stigma was also observed. Rarely the hawkmoths approached the flowers from the side, inserting their proboscides through the peripheral filaments directly to the flower base. In this orientation they were still dusted with pollen but did not contact the stigma.

Since there were no other sphingophilous plants flowering in Kirindy Forest in February, and since hawkmoths did not spend long in each tree, a high level of inter-tree movement is implicated (see Linhart & Mendenhall, 1977). Thus, *Coelonia* is clearly the major pollinator of *A. rubrostipa*.

Two species of nocturnal lemur (*Cheirogaleus medius* and *Phaner furcifer*) were frequently observed visiting *A. rubrostipa* flowers. The lemurs collected nectar non-destructively and also hunted insects (mainly settling moths). On a few occasions the lemurs approached the flowers from the apex and, in doing so, rubbed their vents over the anthers and stigma (as depicted for *A. za*, Fig. 20). However, they usually approached from the flower stalk and thus did not deposit pollen on the stigma (Fig. 14). Individual lemurs frequently spent several hours in a single tree, but some movement between trees was observed. Both lemurs are potentially capable of bringing about some pollen transfer, though this might be lower in *Phaner*, which engaged in periodic bouts of grooming and probably removed some of the pollen. Since both species take large amounts of nectar and cause some damage to flowers, their overall effect on reproductive output could be negative.

Diurnal insects such as bees and flies made rare visits in the morning after anthesis but these did not effect pollination. At night, ants and settling moths congregated on the calyx of newly opened flowers (Fig. 2E). In view of the long nectar-to-stigma distance (usually at least 20 cm), these visits did not result in pollination. No damage to floral tissue was observed, but it is unclear whether these animals are nectar thieves (collecting nectar that would otherwise serve as an attractant for legitimate pollinators) or commensals (collecting excess nectar).

In only one case was a Madagascar green sunbird (*Nectarinia notata*) seen visiting a flower, and this was a brief non-pollinating visit lasting 2 seconds.

(6) Adansonia madagascariensis. The study site for the work on *A. madagascariensis*, Montagnes des Français, is heavily disturbed, and this could explain the low frequency of floral visitation observed. The only reliable floral visitors to *A. madagascariensis* were honeybees, which collected pollen from the flowers as they were opening in the late afternoon. As the flowers opened there was a brief period when the spreading calyx lobes formed an open-ended tube extending from just below the stigma down to the anthers. At this time, bees foraging for pollen passed close to the stigma and, thus, bee-pollination was a possibility. However, the brevity of this period (approximately 5 minutes) mitigates against cross-pollination. Further work in less disturbed localities is needed to document the pollination system of *A. madagascariensis*.

(7) Adansonia za. The main pollinators are long-tongued hawkmoths, especially *Coelonia solanii* (Fig. 15). This hawkmoth visited the flowers at a steady rate throughout the night with up to 12 visits/flower/hr. Two other species, *Coelonia brevis* R. & J. and *Panogena jasminii* Boisduval, visited the flowers just after dusk and just before dawn. These species have relatively short proboscides (ca. 10 cm; Wasserthal, 1993), and when visiting flowers, they often approached from the side or lighted on the petals. These behaviors are not well suited to pollination, because contact with

FIGURES 18–20. Lemur (*Phaner furcifer*) visits to *Adansonia za*.—18. A lemur chewing a hole in the annular nectar chamber.—19. A lemur ingesting pollen—20. An example of a visit that could effect pollination.

the stigma is only rarely made. In contrast, *Coelonia* has a longer proboscis (14.6–22.3 cm; Nilsson et al., 1987), which permits it to hover in front of the flower while feeding. During visits, the wings and body of hovering moths made frequent contact with the anthers and stigmas. Furthermore, moths spent only a limited amount of time in a tree, suggesting that they move between trees, thereby permitting cross-pollination.

As well as hawkmoths, fork-marked lemurs (*Phaner furcifer*) were frequent visitors. A group of five individuals visited the same tree on several nights, following one another through the canopy approximately one minute apart. They predominantly fed on nectar, licking the calyx and petal bases (as Fig. 14). They were usually non-destructive, but sometimes chewed open the nectar chamber (Fig. 18), although this did not lead to visible damage to the gynoecium. Some animals were observed to lick the anthers directly (Fig. 19), apparently ingesting pollen. To my knowledge this is the first report of active pollen-feeding in *Phaner*, and the possibility that lemurs digest pollen should be considered (previously reported in nectarivorous marsupials (Turner, 1984) and bats (Howell, 1974)).

As with *A. rubrostipa*, most lemur visits did not result in contact with the stigma. However, a few times an animal approached from another branch, rubbing its front against the anthers and stigma (Fig. 20) and this behavior could lead to pollination. Overall, *Phaner* removes large quantities of both nectar and pollen and deposits relatively small amounts of pollen on stigmas. Furthermore, grooming, which could reduce the amount of pollen carried from tree to tree, was observed. Detailed studies are thus needed to determine whether the net effect of lemurs on the reproductive output of baobabs is positive (due to pollination) or negative (due to pollen/nectar theft). It is clear that even if they have a net positive effect it is less than that provided by hawkmoths.

Pollen collection by bees occurred in the morning. These visits were directed exclusively at the anthers and thus resulted in little or no pollination. Bees are probably commensals, having no negative effect on baobab fitness.

Butterflies occasionally landed at the bases of flowers in the early morning, apparently collecting nectar. They are minor nectar-thieves with either a neutral or negative effect on the trees, depending on the potential for nectar reabsorption.

The large diurnal lemur *Propithecus verreauxi verreauxi* A. Grandidier fed destructively on floral buds and flowers. However, like the other diurnal visitors, they do not contribute to pollination. Thus, it can be concluded that *A. za* is predominantly pollinated by long-tongued hawkmoths with some minor role perhaps being played by nocturnal lemurs.

(8) Adansonia perrieri. The main pollinators of *A. perrieri* are long-tongued sphingids, *Coelonia solanii* (Fig. 16) and *Xanthopan morgani* Walker (Fig. 17), which have bodies of 5–6 cm and proboscides exceeding 20 cm. *Coelonia* is the main pollinator of *A. za* and *A. rubrostipa*, whereas *A. perrieri* is the only baobab I observed being visited by *Xanthopan*. *Xanthopan* is, however, an important pollinator in Madagascar (Nilsson et al., 1985, 1987) and is the subspecies predicted to exist by Darwin (1862).

Most visits by hawkmoths occur just after dusk, with many fewer later in the night. Moths hover in front or slightly to the side of the flowers and insert their long proboscides through the petal bases to reach the nectar (Fig. 17). Each visit lasts 1–2 seconds, but a moth will occasionally visit a flower several times in quick succession. The visitation rate varied greatly from night to night and from tree to tree. The peak observed was approximately one visit/flower/min. for 20 minutes. At times, moth activity was so intense that moths engaged in aggressive interactions in order to gain access to flowers. This intense foraging occurred when there were only limited resources available to hawkmoths due to the almost simultaneous cessation of flowering of several hawkmoth-pollinated plants in the forest (Solanaceae—*Datura* sp., Meliaceae—*Turraea* sp., and an unidentified Amaryllidaceae).

Bees and butterflies were observed visiting flowers in search of pollen and nectar, respectively. However, they were infrequent visitors and did not contribute to pollination because of their lack of contact with stigmas. The only vertebrate flower visitors were sunbirds (*Nectarinia souimanga*), which occasionally visited in the early morning. They drank nectar while perching on the flower stalk and did not contact the anthers or stigmas.

No short-tongued hawkmoths stole nectar, which suggests that they are absent from Montagne d'Ambre in the flowering season. Thus, long-tongued hawkmoths were the only animals observed visiting *A. perrieri* flowers in a manner conducive to pollen-transfer.

Discussion

Looking at the genus as a whole, it is clear that *Adansonia* manifests a considerable diversity in its floral biology, much of which reflects interspecific differences in pollination biology. Now that the

pollination and floral biology of the extant species of baobab is documented (with the exception of *A. madagascariensis*), the next challenge is to elucidate the evolutionary mechanisms that have led to this floral diversity. A number of specific questions need to be asked. To what extent has natural selection acted on individual floral traits in regard to improved pollination by the current pollinating agents? That is to say: what floral traits are adaptations sensu Gould & Vrba (1982)? Likewise, what floral traits are exaptations: traits that have utility under the current pollination system but evolved for some other reason? Furthermore, which phenotypic traits evolved as developmental by-products of selection acting on other parts of the flower?

As Gould & Lewontin (1979) and Gould & Vrba (1982) pointed out, these questions are intrinsically historical and cannot be answered by looking at current configurations alone. We need some knowledge of the evolutionary history. In the case of *Adansonia* we need to know whether mammal- or hawkmoth-pollination is ancestral and when various floral characters evolved with respect to the switch in pollination system (Greene, 1986; Baum & Larson, 1991). Fossil evidence is unavailable, so the only source of such information is phylogenetic analysis. In the future I hope to evaluate the adaptive status of many floral characters using a phylogenetic approach (see Baum & Larson, 1991). A prerequisite for such a study is a set of clearly defined adaptive hypotheses. In the remainder of this paper I highlight characters that seem to "fit" the physical, behavioral, and sensory attributes of the pollinating animals and propose them as hypotheses of adaptation. I stress that these are just hypotheses. If they appear speculative at times it should be remembered that my purpose is to focus attention on interesting areas for further research rather than to imply that adaptation prevails in shaping the floral biology of *Adansonia*.

SECTION *BREVITUBAE* AND SECTION *ADANSONIA*

The data for section *Brevitubae* suggest both species are primarily pollinated by mammals. Fruit bats play the major role in *A. suarezensis*, but in the case of *A. grandidieri* nocturnal lemurs are the main pollinators, at least in the vicinity of Marofandelia. Although lemurs have been shown to be important pollinators of some Malagasy plants (Nilsson et al., 1993; Kress et al., 1994) and non-flying mammals have been shown to pollinate some Bombacaceae species in the Neotropics (Prance, 1980; Janson et al., 1981; Steiner, 1981; Gribel, 1988), bat-pollination elsewhere in the range of *A. grandidieri* cannot be ruled out.

Potential nectar and pollen thieves in section *Brevitubae* include bees, sunbirds, hawkmoths, and possibly nocturnal lemurs. Overall, these data suggest a great similarity between the pollination system of sections *Brevitubae* and *Adansonia*. Bats are the major pollinators of *A. digitata*, whereas hawkmoths are thieves, and bushbabies play similar roles to the nocturnal lemurs in Madagascar (i.e., they are either minor pollinators or nectar thieves).

Several characters of sections *Brevitubae* and *Adansonia* seem suited equally to pollination by bats and non-flying mammals. Nocturnal, pale-colored flowers with musky scent and copious nectar are typical of both bat- (Faegri & van der Pijl, 1979) and non-flying-mammal-pollinated plants (Janson et al., 1981; Turner, 1982, 1983; Weins et al., 1983; Rebelo & Breytenbach, 1987). Similarly, the large pollen : ovule ratio (relative to *Longitubae*) has been suggested to be favorable for bat-pollinated plants due to the large surface area of the pollinators (Heithaus et al., 1974), and a similar line of reasoning would apply to non-flying mammals.

Fruit bats are large, not particularly agile flyers and plants pollinated by them frequently have easily accessible flowers (van der Pijl, 1941; Marshall, 1983). In section *Adansonia* this is achieved by penduliflory, whereas in section *Brevitubae* the flowers are borne on erect, sturdy stalks and the crowns have a flat-topped, "pagoda" form that is common in bat-pollinated trees (Marshall, 1983). These alternative "solutions" seem in turn to account for several of the other morphological differences between the flowers of these sections. For example, *A. digitata* has broad petals on which the nectar accumulates, whereas in *A. grandidieri* and *A. suarezensis* it collects in the cup-shaped calyx. Also, the two flower positions can be assumed to affect the behavior of floral visitors. Penduliflory is especially suited to fruit bats, which generally approach from below and land head-up on flowers (Hopkins, 1983, 1984). However, penduliflory must limit accessibility to bushbabies and other non-flying mammals. Erect flowers, on the other hand, might perhaps be handled less efficiently by bats (this is not known), but are probably more accessible to lemurs.

The phenology of section *Brevitubae* seems suited to mammal pollination. The dry season in Madagascar is a period of low availability of food (Petter

et al., 1975; Hladik et al., 1980), making baobab nectar a significant resource, and thereby encouraging visits by animals active at that time of year.

The rapid anthesis of bat-pollinated baobabs around dusk can be hypothesized to serve the biological role of reducing pollen and nectar loss to diurnal animals (e.g., bees and sunbirds) while allowing nectar presentation to primarily crepuscular paleotropical fruit bats (Baker, 1973; Marshall, 1983). However, the synchronization of anthesis with dusk seems less critical for lemur pollination, as both *Phaner furcifer* and *Cheirogaleus medius* foraged throughout the night.

SECTION *LONGITUBAE*

The pollination observations in section *Longitubae* suggest that these species manifest a radically different pollination system from that of the other sections. All species for which adequate data exist had long-tongued hawkmoths as their major pollinators. Bats were never involved and nocturnal lemurs were only observed to visit *A. rubrostipa* and *A. za*, where their visits did not contribute significantly to pollination. Nectarivorous birds were nectar thieves, although honeyeaters could be minor pollinators of *A. gibbosa* in Australia. Insects such as settling moths, ants, and bees were commensals or parasites, contributing no pollination. The pollination biology of *A. madagascariensis* remains unresolved, but long-tongued hawkmoths are the most likely pollinators given the general similarity of the floral morphology to *A. za* and other Malagasy *Longitubae*.

Section *Longitubae* has numerous characters that appear well suited to pollination by sphingids. The flowers are nocturnal and sweet-smelling and the androecium is pale and highly visible. The nectar is less copious than in the mammal-pollinated species and is well protected in the tubular calyx. The petal bases overlap, limiting access to the nectar, and the inner surface of the calyx has stiff, upward-pointing hairs making it difficult to obtain nectar from outside the petals. Instead, hawkmoths must obtain nectar by inserting the proboscis inside the petals (i.e., along the outside of the staminal tube) and into the nectar chamber through one of the five narrow openings between the petal bases. The concealment of the nectar means that short-tongued, settling insects can extract little, if any, nectar.

The flowers of section *Longitubae* are elongated, with a stigma-to-nectar distance similar to or longer than the proboscis length of the pollinating sphingids. As originally argued by Darwin (1862) and refined by Nilsson (1988), hawkmoths do not approach flowers closer than is necessary to acquire nectar. Hence, flowers significantly shorter than the moth's proboscis have no opportunity to deposit pollen on the insects' wings and bodies. Darwin (1862) also proposed that a hawkmoth whose proboscis is longer than the flower will be able to remove more nectar (but note Wasserthal's (1993) alternative explanation for the evolution of long proboscides). Taken together these forces can theoretically lead to a co-evolutionary "arms race" between sphingids and sphingophilous flowers which, it is argued, accounts for the extremes of proboscis and flower length found in some areas, including Madagascar. It seems likely that, as major nectar resources, Malagasy baobabs have played some part in this co-evolutionary spiral.

Relative to sections *Brevitubae* and *Adansonia*, section *Longitubae* has a low pollen:ovule ratio and highly versatile anthers. These features can each be hypothesized to be adaptive given the small size of hawkmoths relative to bats and lemurs. With a smaller surface area hawkmoths will become saturated with less pollen (see Heithaus et al., 1974) and with a smaller mass they will dislodge pollen from anthers less easily. Versatile anthers generally release pollen more easily than adnate or basifixed ones (note the tendency for versatile insertion in wind-pollinated plants) and thus are possibly adaptations to hawkmoth pollination.

Differences in androecial structure within *Longitubae* are hard to explain. However, the central bundle of *A. rubrostipa* can be viewed as a specialization that increases the number of anthers at the center of the flower where most hawkmoths hover while extracting nectar.

Wet-season flowering is usual in hawkmoth-pollinated plants, as the early wet season represents a peak in hawkmoth abundance and few moths are active during the dry season (Owen, 1969; Nilsson et al., 1985; Haber & Frankie, 1989).

As with bats, hawkmoths show a peak of activity soon after dark, probably due to temperature constraints on foraging (Cruden et al., 1976). Thus, like the mammal-pollinated species, the hawkmoth-pollinated baobabs benefit by rapid anthesis at dusk. The spectacularly rapid anthesis found in *A. rubrostipa*, *A. za*, and *A. madagascariensis* could have arisen through direct selection or alternatively as a developmental by-product of their extremely elongated flowers.

The Malagasy *Longitubae* differ strikingly from the remaining baobabs by their red and yellow floral

pigments. All four species have yellow or red petals, a red or pink inner calyx (whitish in some *A. perrieri*), and a red style. In searching for an adaptive hypothesis for this pigmentation it is noteworthy that many tropical hawkmoth-pollinated plants have reddish styles or filaments (Haber & Frankie, 1989). The limited studies of hawkmoth vision suggest that they see poorly at the red end of the visual spectrum (Knoll, 1922). It can thus be suggested that the red coloration "camouflages" the reproductive structures and thereby increases the frequency with which moths bump into them during nectar-feeding. Haber & Frankie (1989) made a similar suggestion to account for the presence of magenta filaments in some hawkmoth-pollinated *Calliandra* and *Capparis*. The red inner surface of the calyx can similarly be viewed as a means of discouraging insects from visiting the base of the flower and extracting nectar from outside the corolla (thereby avoiding pollination). The red petals of *A. madagascariensis* and the reddish blush on those of some *A. za* are, however, hard to explain adaptively, although the corolla plays a subsidiary role in the androecium in the visual display of section *Longitubae*. Likewise, it would be rash to hypothesize any adaptive value to the yellow corolla of many Malagasy *Longitubae*, as this could be a pleiotropic effect of the genes leading to a red style and calyx.

FUTURE WORK

Understanding the mechanisms that have led to floral diversity in *Adansonia* requires much further work. The pollination ecology of *A. madagascariensis*, *A. suarezensis*, and *A. grandidieri* would benefit from further study; additional studies of floral biology in these and other species would, likewise, be useful, especially on nectar production, nectar contents, and breeding systems. Also, studies of floral development would help evaluate phylogenetic/developmental constraint. Ultimately, such detailed understanding of the floral and pollination biology of extant baobabs and their close relatives in the Bombacaceae can be integrated with a robust phylogeny to gain insight into the relative roles of adaptation (direct selection), exaptation (co-option of characters for new roles), and developmental/phylogenetic constraint in the evolution of flowers.

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